

Low reproductive success of the Carrion Crow *Corvus corone corone* - Hooded Crow *Corvus c. cornix* hybrids.

Nicola Saino

Dipartimento di Biologia, Sezione di Zoologia-Scienze Naturali
Via Celoria 26, 20133 Milano Italy

Abstract. The reproductive success of pairs of different assortments was studied in an area of intergradation between Carrion Crow and Hooded Crow in north-Western Italy during spring 1989. No significant variation in the mean size of the clutches laid by female carrion crows, hooded crows and hybrids was observed although hybrid females tended to lay fewer eggs. Female phenotype significantly influenced the number of chicks fledged; the nests of hybrid females produced on average significantly less chicks than nests of the parental females. No significant variation in the mean number of chicks fledged was observed among nests of Carrion Crow, Hooded Crow and hybrid males. Evidences of assortative mating were observed; parental phenotype tended to mate with individuals of their phenotype and avoided inter-phenotype mating. The results suggest that the 'dynamic equilibrium model' could partly explain the phenomena in the hybrid zone studied. However, some aspects of the dynamic of the Carrion/Hooded crow hybrid zone need to be examined more closely. A comparative analysis of the reproductive biology of sympatric and allopatric populations of the Carrion Crow and of the Hooded Crow and the analysis of other aspects of Crows biology in the hybrid zones are also needed.

Key words: assortative mating, *Corvus corone cornix*, *Corvus corone corone*, hybrids, Italy, reproductive success

Hybrid zones are relatively narrow regions in which populations that have diverged genetically, meet, mate and produce hybrids (Barton & Hewitt 1985). Hybrid zones are often interpreted as due to a secondary contact, following a period of geographical isolation, or as the result of parapatric divergence (Short 1969, Moore 1977)

Three hypotheses have been formulated to explain the existence of apparently stable hybrid zones.

The first states that they are ephemeral phenomena: their stability is apparent to the short-lived observer and they will evolve in either of two opposite directions:

a) if the divergence between the parental populations has progressed to the extent that hybridization will disrupt the 'harmony of distinctly coadapted gene complexes' (Moore 1977) the hybrid zone will become more restricted or extinct as pre-zygotic isolating mechanisms evolve through selection against hybrids; b) if divergence and coadaptation of gene complexes in the two populations has not progressed to the extent that hybridization would result in hybrid unfitness or hybrid breakdown, the hybrid zone will expand in width through introgressive hybridization (Remington 1968).

In a second hypothesis, which is usually referred to as 'bounded hybrid superiority' (Moore & Koenig 1986), the hybrid zones persist because they coincide with ecotones in which hybrids are at least as fit as the parental populations. The superiority of the hybrids is 'bounded' to the ecotone.

The third hypothesis is the 'dynamic equilibrium model' (Barton 1979, Barton & Hewitt 1981): hybrids suffer depressed fitness, in respect to the parental populations, which prevents the hybrid zone from broadening through introgressive hybridization. Although in the hybrid zone natural selection will favour individuals prone to avoid hybridization, the parental populations outside the hybrid zone will not experience such a selective pressure. Hybrid zones are maintained by a dynamic balance between selection against hybrids and dispersal from the areas of allopatry towards the hybrid zone.

Many examples of populations of bird species that have diverged to some extent and show parapatric distributions with relatively narrow zones of intergradation, have come to light in last decades (see for example Rising 1983). Probably one of the first hybrid zones to be described has been that between Carrion Crow and Hooded Crow (*Corvus corone corone* and *Corvus corone cornix*) in central and northern Europe (Meise 1928, Mayr 1963). Carrion and Hooded crow are parapatrically distributed in Scotland, in Central Europe and in the Alps (see Mayr 1963).

Surprisingly no adequate attention has been devoted to the phenomena that occur within the crow hybrid zone trough Europe.

In this paper I present preliminary evidences that some Carrion/Hooded hybrids experience low reproductive success as compared to the parental phenotypes within a crow hybrid zone in the Alps.

STUDY AREA AND METHODS

The study was carried out in Spring 1989, in an area of Cuneo province (Piedmont, NW Italy) where Carrion Crows and Hooded Crows live in sympatry and intergrade. I actively searched for nests in an area about 220 km² wide. When the nests were found they were mapped. I visited the nests usually at least six days later they were found. The parents of each nest were scored into Carrion crows, Hooded crows and hybrids according to their phenotype. Since F1 hybrids were indistinguishable from subsequent hybrid generations and back-crosses I was forced to consider as belonging to the same phenotypic hybrid category all the individuals that exhibited plumage with characteristics intermediate between the parental morphs (see Melde 1984 for a description of parental and hybrid phenotypes). Of each nest I recorded, when possible, the clutch size and the number of chicks fledged. Some nests were found after hatching and for these nests only the number of chicks fledged is available.

Fully detailed methods will be published elsewhere (Saino in prep.). The expected relative frequencies of occurrence of the nine possible kinds of pair assortment under the hypothesis of random mating were calculated by means of the following formula:

$$P_{ij} = (X_i * Y_j) * T^{-2}$$

where P_{ij} is the expected relative frequency of occurrence of pair with a ij composition, X_i is the total number of females of the i -th phenotype in the sample, Y_j is the number of males of the j -th phenotype and $T (=56)$ is the number of pairs of which both female and male were known.

RESULTS

Overall, 58 nests were studied. The composition of the breeding pairs is reported in Table I.

No significant variation was found in the mean size of the clutches laid by the females of the three phenotypes ($F_{2,46}=1.04$, $P=0.36$; Fig. 1). No significant differences in clutch size were observed by contrasting the parental phenotypes ($F_{1,36}=0.38$, $P=0.55$) nor by contrasting the parental phenotypes to the hybrids although hybrids tended to lay fewer eggs ($F_{1,17}=1.75$, $P=0.19$).

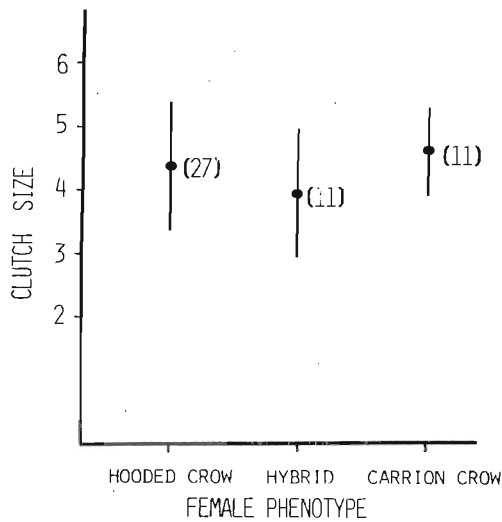


FIGURE 1. Mean for the size of the clutches laid by females of the three phenotypes; bars show standard deviations. In parentheses the size of the samples.

One-way analysis of variance revealed an almost significant variation of the breeding success (i.e. the number of chicks fledged) among the 3 female phenotypic categories ($F_{2,55}=2.79$, $P=0.07$; Fig. 2). No significant difference in the reproductive success was observed between the parental females ($F_{1,45}=0.18$, $P=0.68$) whereas a significant difference emerged by contrasting the parental female phenotypes with the hybrid females ($F_{1,56}=5.5$, $P=0.023$). The phenotype of the male had not effect on the reproductive success of the breeding pairs ($F_{2,53}=0.061$, $P=0.94$).

Some evidences of the reduced reproductive success suffered by certain hybrids were collected for 4 out of the 11 nests of hybrid females:

1) one pair (male and female both hybrids) completely failed to hatch the three eggs. The eggs were completely depigmented and had a very thin shell. Two of them were found broken since several days when the nest was visited for the first time. The third was found broken at the time of the second visit. No similar abnormalities in egg shell thickness and pigmentation were found within the hybrid zone in parental nests nor in a sample of 359 eggs from a population of hooded crows about 150 km apart in the Po Valley.

2) one pair (hybrid female x hooded male) failed to hatch eggs. The eggs were very small and two of them were depigmented, possibly with thin shells. Small pieces of egg shells were found when the nest was visited for the second time. Apparently the nest had not been preyed upon.

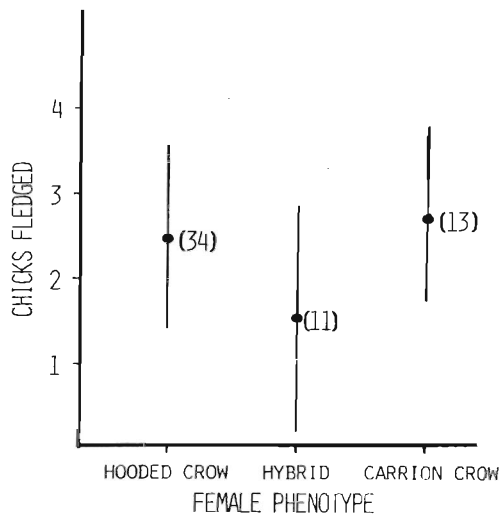


FIGURE 2. Mean for the number of chicks fledged from nests of females of the three phenotypes; bars show standard deviations. In parenthesis the size of the sample

3) in two nests of hybrid females the fifty per cent of the chicks (two in one nest, one in another nest) died when they were older than 13 days; in parental nests the mortality at this age was lower.

No statistical analysis of the combined effects of female and male phenotypes on the reproductive success was performed because of the very small sample for some of the pair assortments (Tab. I).

The observed frequency distribution of the nine possible pair compositions significantly differed from the frequency distribution expected under the hypothesis of random mating among phenotypes (Tab. I).

DISCUSSION

The results show that on average hybrid females have a significantly lower reproductive success as compared to the parental female phenotypes and that some hybrid females do experience peculiar reproductive "maladies" which are not shared by the parental phenotypes. Assortative mating seems to occur within the hybrid zone since parental phenotypes tend to mate more often than expected under the hypothesis of random encounters with individuals of their phenotype and to avoid inter-phenotype mating. Data indicating assortative mating must be considered with caution since they do not take into account that the relative frequency of the phenotypes changes across the hybrid zone. However, the extent of the disagreement between the observed and the expected frequencies of occurrence of the pair compositions in the breeding population studied suggests that parental individuals do not mate at random with the other phenotypes.

Table I. Observed and expected composition (See 'Methods') of 56 breeding pairs. C=Carrion crow, I=hybrid, H=Hooded crow. In parenthesis the pairs of which only the female was determined.

FEMALE	MALE	observed frequency	expected frequency	χ^2
C	C	11 (+1)	3.4	16.99
C	I	0	1.1	-
C	H	1	7.5	5.63
I	C	2	3.1	-
I	I	2	1.0	-
I	H	7	6.9	0.0
H	C	3	9.4	4.36
H	I	3	3.0	-
H	H	27 (+1)	20.6	1.99
CI,IC,II,HI POOLED		7	8.1	0.15
				$\chi^2=29.12$
				d.f.=5
				P<0.001

Thus, both pre-and post-zygotic isolating mechanisms seem to act in the alpine crow hybrid zone. These findings are inconsistent with those of Picozzi (1976) who did not find any evidence of assortative mating and reduced fitness of the hybrids in the Scotland.

However, the Scottish and the hybrid zone I studied seem to be rather different at least in three respects:

1) in Scotland the hybrid zone is much wider than in the Piedmont (Sharrock 1976)

2) the frequency of hybrid phenotypes within the hybrid zone is sensibly higher in Scotland than in the Alps (Picozzi 1976)

3) in Scotland the hybrid zone has been moving during the last 50 years whereas no such evidence existS for the Alps.

These preliminary data weakly support the idea that the Carrion/Hooded crow hybrid zone in the Alps could be maintained by a dynamic equilibrium between the depressed reproductive success of the hybrids and dispersal and that some indirect evidence of reinforcement of pre-mating isolating mechanisms exists. However, further studies are needed in order to solve some crucial points; in particular:

1) what does prevent the hybrid zone from flowing geographically? Barton (1979) showed that hybrid unfitness itself can fix the width and that demographic fluctuations could guarantee the geographic stability of the hybrid zones. Observations (Saino in prep.) on the foraging habitats of the different phenotypes in the area of sympatry suggest that a more simple explanation of the geographic stability could be formulated. The hybrid zone in Piedmont coincides with a narrow area running just at the base of the Alps. Each of the parental phenotypes could be better adapted than the other to environmental conditions in its range and the phenotypes could differ in foraging habitat preferences (Saino in prep.). This could force the two phenotypes in distinct ranges that share a narrow zone of overlap. Indeed, Carrion crows and Hooded crows inhabit very different habitats in western Italy. The former is mainly restricted to valleys with predominant pastures and meadows whereas the latter inhabits mainly intensively cultivated lowlands.

2) Is the 'dynamic equilibrium model' (Barton & Hewitt 1981) sufficient to explain the persistence of the narrow Carrion/Hooded crow hybrid zone or is it an oversimplification of the mechanism that promote the maintenance of the crow hybrid zone? My results show that hybrid females, on average, experience lower reproductive success and possibly lower fitness than the parental populations in the hybrid zone. Indeed, many hybrid females have a reproductive success similar to that of the parental females thus indicating that selection against hybrids and back-crosses operates differentially on different hybrid genotypes. Hybrids which exhibit a 'normal' reproductive success may contribute by themselves to the maintenance of a hybrid zone. Furthermore, selection seems to operate differentially on hybrid males and females since, as I showed, male phenotype does not affect the reproductive success.

3) Is reproductive success a good estimate of the fitness of a breeding pair? Richner (1989) has shown that the ability of an individual to acquire a territory and a mate in carrion crows depends on its size which is at least partly ontogenetically controlled. The reproductive success could be a biased estimate of the individual fitness of the parents.

ACKNOWLEDGEMENTS

I am grateful to S. Villa and to M. Schlueter for help in field work

SOMMARIO.

Evidenze di ridotto successo riproduttivo negli ibridi di Cornacchia grigia e Cornacchia nera

- Sono esposti dati preliminari riguardanti il successo riproduttivo e la composizione delle coppie in un'area di intergradazione fra Cornacchia nera *Corvus corone corone* e Cornacchia grigia *Corvus corone cornix* in Italia nord-occidentale (Piemonte, Provincia di Cuneo).

- Non è stata riscontrata una variazione significativa nella dimensione media delle covate deposte da femmine con fenotipo parentale e da femmine ibride, benchè queste ultime abbiano deposto mediamente circa 0,5 uova in meno delle femmine parentali. Il fenotipo della femmina ha influenzato significativamente il successo riproduttivo (=numero di pulcini involati); i nidi di femmine fenotipicamente ibride hanno prodotto significativamente meno pulcini dei nidi di femmine parentali. Il fenotipo del maschio non ha influenzato il successo riproduttivo. Sono inoltre emerse evidenze di assortimento non casuale delle coppie; gli individui di un fenotipo erano più frequentemente di quanto atteso accoppiati ad individui del loro stesso fenotipo. I risultati suggeriscono che il modello dell'equilibrio dinamico fra selezione contro gli ibridi e dispersione dalle aree di allopatria verso la zona di ibridazione si adatta a quanto osservato nella area di ibridazione fra cornacchia nera e cornacchia grigia. Alcuni aspetti della dinamica di questa zona di ibridazione e una analisi comparativa della biologia riproduttiva delle popolazioni di Cornacchia nelle zone di ibridazione e in aree di allopatria necessitano tuttavia di ulteriori indagini.

FIG. 1. Medie del numero di uova deposte da femmine appartenenti alle tre categorie fenotipiche. Hooded crow=Cornacchia grigia, hybrid=ibridi, Carrion crow = Cornacchia nera. Fra parentesi la dimensione dei campioni.

FIG. 2. Medie del numero di pulcini involati da nidi di femmine delle tre categorie fenotipiche Hooded crow=Cornacchia grigia, hybrid=ibridi, Carrion crow = Cornacchia nera. Fra parentesi la dimensione dei campioni.

TAB.I. Composizione osservata e attesa delle 56 coppie di cui sono stati identificati entrambi i componenti. C=Cornacchia nera, I=ibrido, H=Cornacchia grigia. Fra parentesi le coppie di cui la sola femmina è stata identificata.

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Ricevuto il 3 agosto 1990.